Feeding and the epiphyte food resources of gastropods living on leaves of the seagrass *Amphibolis griffithii* in south-western Australia

by
John Nielsen and Roger Lethbridge

School of Biological and Environmental Sciences
Murdoch University, Murdoch, W. Australia 6150

ABSTRACT

This paper reports the radula structure and diets of trochid (*Thalotia conica*, *Prothalotia lehmanni*) and columbellid (*Pyrene bidentata*) gastropods that reside amongst the terminal leaf clusters of the seagrass, *Amphibolis griffithii*, in shallow, subtidal regions of south-western Australia. Both trochids possessed similar rhipidoglossan radulae that swept diatoms, small encrusting coralline algae and other organisms from the seagrass leaves. *Pyrene bidentata* used similar food resources but also consumed some larger food fragments (e.g. hydroid colonies) with its rachiglossan radula.

Snail diets most closely reflected the range and abundance of epiphytes on leaves in summer. During particularly the winter, certain diatoms were disproportionately present in snail diets, either through active food selection or because some diatoms were patchily distributed on leaves. Although unidentifiable materials accounted for about 20-35% by volume of food present in snail stomachs, our data support the view that epiphytes can be more important than detritus in sustaining the food webs of vagile gastropods in seagrass ecosystems.

INTRODUCTION

Seagrass leaves markedly increase the effective surface area of benthic environments (Kikuchi & Peres, 1977) and provide a natural substratum for colonization by a broad range of epiphytic organisms (Ducker, Foord & Knox, 1977; Harlin, 1980). The primary productivity of seagrass meadows is therefore partitioned between the macrophytes and their epiphytes, with energy passing from this community to higher trophic levels by more than one route.

Living seagrass leaves are typically consumed by only a few herbivorous fish (Randall, 1967; Carr & Adams, 1973; Pollard, 1984), crustaceans (Klumpp &

Nichols, 1983) and turtles (Bjorndal, 1980, for Caribbean habitats), and much of the leaf material is thought to enter food webs via detrital pathways (Fenchel, 1970). However, bacteria, diatoms and small epiphytic algae are often abundant on leaves (Novak, 1984), very highly productive (Morgan & Kitting, 1984; Kitting, Fry & Morgan, 1984), and directly available to microphagous browsers in the seagrass canopy. Thus, gammarid amphipods exhibit distinct dietary preferences for different resources in seagrass meadows (Zimmerman *et al.*, 1979), and crustaceans and gastropods feed selectively on the epiphytic flora associated with the leaves of *Thalassia* and *Halodule* (Kitting, 1984; Kitting *et al.,* 1984), *Zostera* (van Montfrans *et al.,* 1982) and *Heterozostera* (Howard, 1982).

In south-western Australia many shallow, subtidal regions are dominated by extensive meadows of *Posidonia* and *Amphibolis* that support an abundant gastropod fauna. This paper reports the epiphytes ingested by trochid (*Thalotia conica, Prothalotia lehmanni*) and columbellid (*Pyrene bidentata*) gastropods that occur at moderate to high population densities, i.e. 50->200 snails m-², amongst the terminal leaf clusters of *Amphibolis griffithii.*

MATERIALS AND METHODS

Thalotia conica, Prothalotia lehmanni and *Pyrene bidentata* were collected from the central region of a large monospecific stand of *Amphibolis griffithii* (depth 3-4 m) near the southern tip of Penguin Island, Western Australia (115⁰ 41' E, 32⁰ 19' S). Seagrasses within 0.25 m-² quadrats were severed at substratum level with scissors and immediately transported to the laboratory where the snails were separated from leaf clusters.

Five radulae were dissected from each species (shell lengths 14-18 mm), fixed in gluteraldehyde and dehydrated in alcohol, mounted in different orientations on aluminium stubs, and sputter-coated with gold for examination with a Phillips 501B scanning electron microscope operating at 30 kv. The central, lateral and marginal teeth were identified and compared with the radula structure of other prosobranch molluscs (Fretter & Graham, 1962; Purchon, 1968; Hickman, 1976; Radwin, 1977). A further 10 radulae from each species were mounted for light microscopy according to methods outlined by Mikkelsen (1985).

The contents of the posterior oesophagus and stomach of 20 snails of each species were examined in February (summer) and July (winter) 1987. The contents of half of these guts were prepared for diatom identifications by boiling in nitric acid followed by repeated washing and centrifugation (Patrick & Reimer, 1966). Each sample was then evenly dispersed on a preheated coverslip and mounted with Hyrax medium when dry. Diatoms were identified to at least generic level from John (1983). The abundance of diatoms of different species in each sample was estimated from counts of 20 non-overlapping fields of view (x400 magnification) per slide. The remaining guts were prepared as above, but omitting HNO_3 treatment, and examined for other animal and plant materials.

Similar methods were employed to identify and estimate the abundance of epiphytes scraped from both surfaces of haphazardly collected leaves in February

and July 1987. A similarity dendrogram based on the Canberra Metric (Clifford & Williams, 1976) was constructed to compare the diversity and abundance of epiphytes on leaves with food materials recovered from snail guts.

During a 48 h period in February 1987, adjacent *Posidionia* and *Amphibolis* meadows were assessed at about 4 h periods to estimate the number of snails associated with stems or terminal leaf clusters (*Amphibolis*), or attached to the apical or basal halves of seagrass blades (*Posidonia*).

RESULTS

Radula Structure

The trochids were equipped with bilaterally symmetrical rhipidoglossan radulae that were similar in overall length and in their total number of tooth rows. They differed from each other principally in the number and arrangement of cusps on their teeth.

In *Thalotia conica*, the central tooth and five sets of lateral teeth were triangular with tricuspid bases. The innermost and tallest marginal teeth possessed a single basal cusp on their outer face but successive groups of these teeth became progressively shorter and ultimately tricuspid at the margins of the radula (Plate 1, 2).

Cusps were absent on the central tooth of *Prothalotia lehmanni* but the first lateral teeth on each side were quadricuspid and tricuspid on their inner and outer faces respectively; all other lateral teeth were basally bicuspid on both faces (Plate 3). As in *T. conica*, the marginal teeth progressively decreased in height, and their outer basal surface varied from unicuspid to tricuspid with increasing distance from the radula midline. The mean relative width of the marginal tooth series, as a ratio compared to the breadth of the central plus lateral teeth, was significantly much greater in *P. lehmanni* than in *T. conica* of similar size (shell length = 14-18 mm; t-test, $p < 0.001$).

Unlike the trochids, the radula in *Pyrene bidentata* was rachiglossan and housed within a protrusible proboscis. It consisted of a central tooth flanked on each side by a single lateral tooth bearing a short series of cusps (Plate 4). Manipulation of the excised radula indicated that the lateral teeth were highly mobile, fanning out when the radula was projected and folding inwards and interlocking when it was withdrawn.

There was a strong positive and linear correlation between radula width and increasing body size (= shell length) in both *Thalotia conica* ($r = 0.894$, $p < 0.001$) and *Prothalotia lehmanni* ($r = 0.936$, $p < 0.001$). Radula width in *Pyrene bidentata* was more weakly correlated with shell length ($r = 0.673$, $p > 0.05$) over the size range measured (Fig. 1).

Epiphytes on *Amphibolis* Leaves and in Snail Diets

The floral community detected on *Amphibolis* leaves was dominated by diatoms (44 species) and the encrusting coralline algae, *Fosliella* sp. and *Pneophyllum* sp.
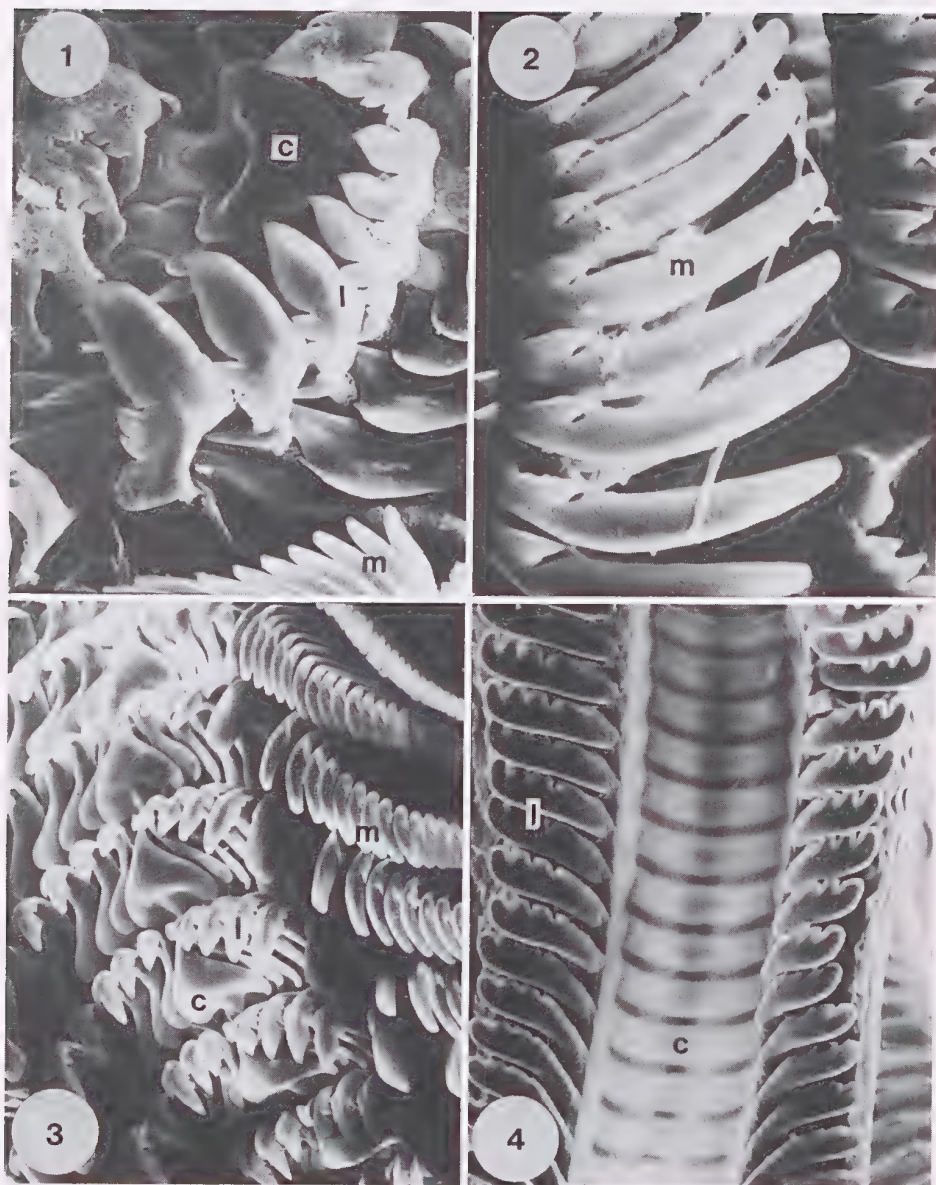
PLATES 1-4: Scanning electron micrographs of parts of the radula of *Thalotia conica* (1,2), *Prothalotia lehmanni* (3) and *Pyrene bidentata* (4) showing the arrangement of the central tooth (c), lateral teeth (L) and marginal teeth (m). Print magnifications are x410 (1), x711 (2), x240 (3) and x147 (4).
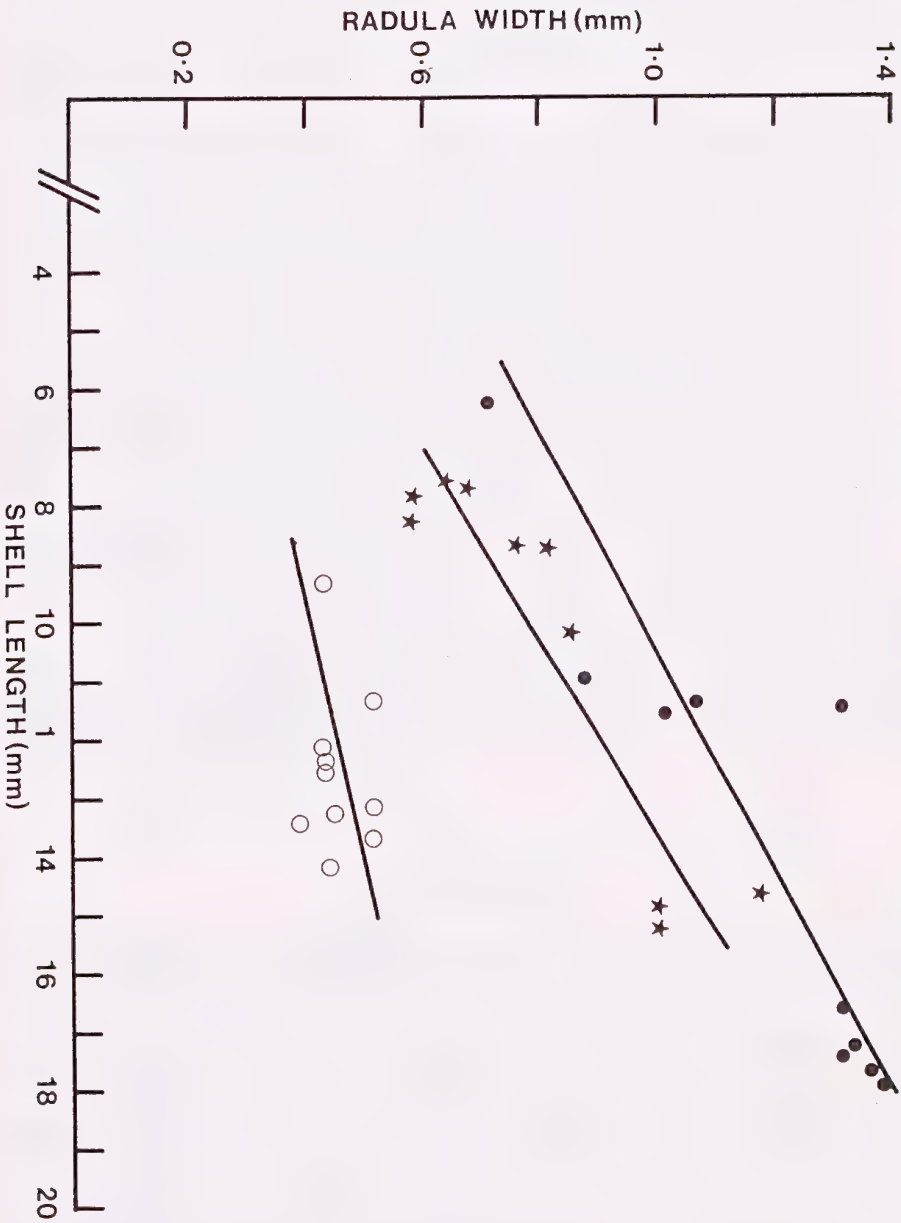
FIGURE 1: Regression lines showing the relationship between total radula width and shell length for *Thalotia conica* (●), *Prothalotia lehmanni* (★) and *Pyrene bidentata* (○). Correlation coefficients and significance values are given in the text.
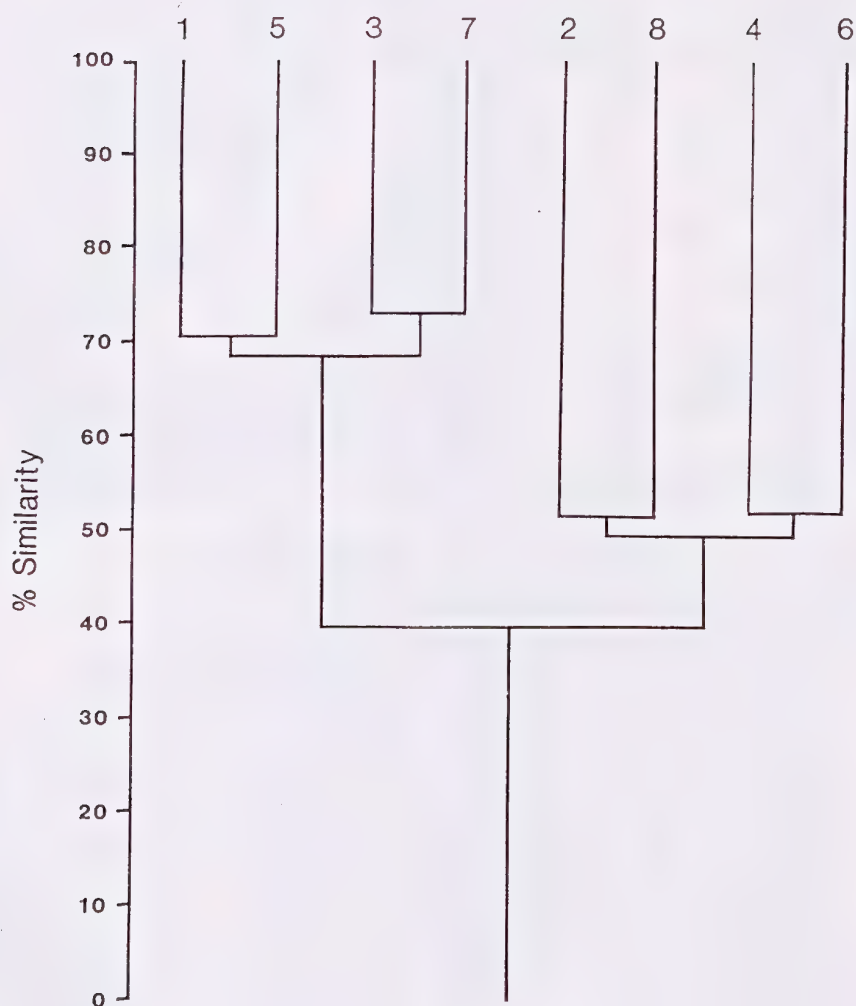
FIGURE 2: Similarity dendrogram showing affinities between gastropod diets and seagrass micro-epibiota. *Amphibolis* leaf epibiota in February (1) and July (2), *T. conica* diet in February (3) and July (4), *P. bidentata* diet in February (5) and July (6), and *P. lehmanni* diet in February (7) and July (8).

(Table 1). The encrusting coralline algae, together with the diatoms *Plagiogramma interruptum*, *Grammatophora oceanica*, *Mastogloia binotata* and *Navicula* sp., were the most abundant species on leaves in both summer and winter. Numerous diatoms (e.g. *Campyloneis grevillei*, *Cocconeis* spp.) persisted at low levels in both seasons whereas others exhibited a marked seasonality and were most abundant in either summer (*Navicula tripunctata*, *Mastogloia* sp. 1.) or winter (*Licmophora* spp., *Mastogloia fimbriata*, *Opephora martyi*). Fourteen species were detected on leaves only during winter, some achieving comparatively high population densities (e.g. *Grammatophora serpentina*, *Rhoicosphenia* sp.). Leaf surfaces were also sometimes occupied by small turf-like or filamentous algae (*Dasya* sp., *Bornetia* sp.), foraminiferans, colonies of hydroids e.g. *Plumularia compressa* and *Campanularia australis*, amphipods, and spicules derived from sponges (Table 1).

Although all diatom species identified on *Amphibolis* leaves were recovered from the stomach contents of the gastropods during this study (Table 1), the diets of the three snails more closely reflected the overall diversity and abundance of members of the leaf epiphytic community in summer than in winter (Fig. 2). Thus, particularly in winter, certain diatoms were more numerous in snail gut contents than they were on the leaves, e.g. *Cocconeis* spp, in *T. conica* and *P. bidentata*, *Gomphonema valentica* and *Mastogloia* sp. 1 in *P. lehmanni*, and *Amphora ventricosa* and *Nitzchia dissipata* in *P. bidentata* (Table 1). This may indicate that some diatoms are preferentially selected by gastropods in certain seasons.

Observations on the vertical migration patterns of snails present on *Posidonia* and *Amphibolis* indicated that the majority of individuals moved up *Posidonia* leaves by day and sought refuge closer to the rhizomes at night. There was, however, no conspicuous pattern of vertical migration of gastropods on *Amphibolis*, and almost all snails were confined to the short, terminal leaf clusters throughout the 48 h observation period.

DISCUSSION

Gastropods in some seagrass meadows undertake vertical diel migrations, seeking cover near the sediments by day and moving upwards towards the epiphyte-laden leaf tips to feed actively at night (Kitting, 1984; Howard, 1987).

Preliminary observations in this study showed a similar pattern of movement by *Thalotia conica*, *Prothalotia lehmanni* and *Pyrene bidentata* in beds of *Posidonia* spp., but failed to detect any marked diel migrations amongst the same snails in adjacent *Amphibolis* stands. These differences may be due to the morphology of the host plants. Thus, whereas many genera of seagrasses have either short or strap-like leaves that arise directly from rhizomes (Den Hartog, 1970), the leaf clusters of *Amphibolis* are borne on the tips of erect, narrow stems (< 330 mm tall at Penguin Island, approx. 2 mm diameter) which may hinder routine vertical migrations. Epiphytes associated with the leaf surfaces therefore represented the major food resource for vagile gastropods in our *Amphibolis* meadow, with snails seeking refuge in the axils of each terminal leaf cluster.

Thalotia conica and *Prothalotia lehmanni* possessed typical rhipidoglossan radulae which are evidently well equipped for "brooming" loosely attached particles from the substratum, a process which relies heavily on the extensive series of marginal teeth (Steneck & Watling, 1982). The strong positive correlation between total radula width and shell length (or age) is presumably related to the essentially herbivorous diet of these gastropods, i.e. growth and maintenance of body size are related to potential food intake and thus to the effective area grazed with each radula stroke. The radula of *P. lehmanni* is narrower than that of *T. conica* at a similar body size, but this may be at least partially compensated for by the significantly greater proportional width of the marginal teeth series in the former species if these are similarly splayed during feeding. With respect to their morphological details, the trochid radulae differed mainly in the number and arrangement of the cusps present on the lateral and marginal teeth but the significance of these small differences is unclear. Identifiable food materials consumed by both trochids were in the same size range (5-235 μm), and there was a considerable overlap in the species composition of diatoms and foraminiferans that they ingested.

Lacking marginal teeth, the rachiglossan radula of *Pyrene bidentata* was only about half the width of that of either trochid (Fig. 2) but bore approximately twice as many rows of mobile and interlocking lateral teeth per unit length. Exhibiting little increase in width with increasing body size, the radula of *P. bidentata* appears to be a more robust and versatile structure for food gathering. Indeed, Bandel (1984) regarded columbellid radulae as ideal tools for cutting, tearing and hooking, features that enable these snails to feed opportunistically on diatoms and filamentous algae as well as animal flesh (Hatfield, 1979; Morgan & Kitting, 1984; Kitting *et al.*, 1984). Despite these attributes, the recognisable food items consumed by *Pyrene bidentata* in this study closely resembled those in the diets of both trochids although it was occasionally able to ingest small hydroid colonies, amphipods and perhaps other small invertebrates. *Pyrene bidentata* is, however, one of the commonest gastropods in numerous intertidal and subtidal localities in south-western Australia, and its dietary range may be much more varied in these other habitats.

A variable proportion of the food consumed by the three gastropods (estimated visually as 20-35% by volume) could not be identified satisfactorily because of the abrasive action of the radula and subsequent digestive processes. However, much of this material appeared to be derived from small filamentous algae (e.g. *Dasya sp., Bornetia* sp.) that are common on *Amphibolis* leaves (Borowitzka & Lethbridge, 1989).

In addition to diatoms, encrusting coralline algae were the most numerous recognisable components in the diets of the three snails, despite the fact that rhipidoglossan radulae have been regarded as poorly equipped to deal with these materials on strictly morphological grounds (Steneck & Watling, 1982). However, these epiphytes (*Fosliella* sp., *Pneophyllum* sp.) form only small confluent plaques on seagrass leaves. Their relatively "brittle" nature and ubiquitous distribution on all but the youngest leaves of *Amphibolis* (Bramwell & Woelkerling, 1984; Harlin *et al.*, 1985) evidently predispose them to becoming common dietary items. Sponge

spicules within the gut contents were essentially detrital elements because poriferans were rare on *Amphibolis* leaves and uncommon on their stems at our sampling station. Most of the spicules present on leaf surfaces probably originated from sponge communities on the limestone reefs that flanked the seagrass meadow.

Our data indicated some changes in the species composition of diatoms in the two seasons examined, and suggested that certain diatoms were favoured dietary items because they were more numerous in the gut contents than on haphazardly collected leaves, especially in winter. In this context, recordings of audible feeding patterns amongst gastropods have shown that feeding starts and stops abruptly as the mouth moves over different foods on seagrass blades (Kitting, 1984). However, foraging selectivity suggested by our data needs cautious interpretation because gut contents could not be related to epiphytes present on any specific leaf, and diatoms may be patchily distributed on seagrass blades. Nevertheless, our data support Kitting's (1984) view that epiphytes can be more important than detritus in sustaining food webs of vagile gastropods in seagrass ecosystems.

ACKNOWLEDGEMENTS

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